PHYLOGENY AND PHYTOGEOGRAPHY

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ABSTRACT

Biogeography is a useful tool for the phylogenist. Distribution patterns, past and present, can be most instructive in indicating possible relationships. This observation is true because the closest living relatives of a phyletically unplaced taxon are more likely than not to be found in the same or adjacent areas rather than on distant continents. However, this generalization must be used with caution for many plant groups possess great vagility and have spread rapidly into appropriate habitats over the earth. The largely Old World Pittosporales are described in some detail as a prime example of application of this dictum of geographic plausibility. Archaic dicotyledons of the Australasian and Asian regions are discussed as other examples of the dictum, as are a few North American taxa such as *Simmondsia,* Crossosomataceae, and *Batis.* Additional angiosperms are listed without discussion for both North and South America.

Key Words: Phylogeny, phytogeography, geographic plausibility, Old World, New World

INTRODUCTION

The two botanical disciplines of phylogeny and phytogeography are interdependent. Correct interpretation of one depends upon considerable knowledge of the other. Certainly in the study of distribution patterns and major disjunctions the plant geographer is heavily dependent upon accurate taxonomy and recognition of monophyletic genetic relationships. Incorrect determinations, mixed labels, and inadequate or inaccurate location data have led many a biogeographer astray. Likewise, the paleobotanist should have a good knowledge of the phylogenetic relationships and the past and present distribution of pertinent taxa to identify the plant fossils that are at hand.

Conversely, knowledge of the present and past distribution of a taxon and its presumed relatives can be critical in determining the phylogenetic relationships of that taxon. Generally the closest living relatives of a phyletically unplaced taxon are more likely than not to be found in the same or adjacent areas rather than on distant continents. This dictum should be used with caution for many plant groups possess great vagility and have spread rapidly into appropriate habitats over the earth's surface. This paper will present some examples of the application of this prin-

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ciple, with especial reference to the Pittosporales (Thorne, 1975, 1976, 1977, 1981, 1983).

<div align="center">PITTOSPORALES</div>

The idea of geographic plausibility became part of my *modus operandi* more than a decade ago as I developed my concept of the Pittosporales (Thorne, 1975). As I was reconstructing what I regarded as natural orders, I had ejected as *taxa incertae sedis* a rather large number of families from many different generally accepted orders because the families obviously did not "fit" in those orders. A group of ten families from the Old World stood out because of their similar distribution patterns and their relatively primitive stem anatomy and floral morphology. Those ten families at that time were treated in five to seven relatively unrelated orders in each of four widely accepted systems of classification (Melchior, 1964; Cronquist, 1968; Takhtajan, 1969; Hutchinson, 1973) involving 16 different ordinal names. The most realistic treatment seemed to me to be that of Hutchinson (1973), with merely five different orders involved and seven families placed in the related Hamamelidales and Pittosporales. Since then I have added three more families to my concept of the Pittosporales.

At present in three current classifications (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1987) the 13 pittosporalean families are still treated in ten, eight, and 12 different orders, respectively. Obviously, my fellow phylogenists do not take into account phytogeographic plausibility in constructing their systems of classification. Conceivably my three suborders, Buxineae, Pittosporineae, and Brunineae, could be elevated into three related orders, Buxales, Pittosporales, and Bruniales, but I can see no need for further subdivision.

To examine this group of families graphically I drew up a chart of their characteristics. I was startled by the large number of salient features that they possessed in common beyond their geographic similarities. Among those characteristics members of my Pittosporales combine usually simple, exstipulate leaves; unspecialized xylem; radially symmetrical flowers with a definite number of stamens opposite the sepals; syncarpous gynoecium; often subapical, pendulous, anatropous ovules; and seeds with minute to linear embryo in abundant endosperm. The species display varied

habit, though most are small trees, shrubs, or twining undershrubs of relatively mesic habitats. They also share in common certain strong tendencies toward dioecism, apetalous or naked flowers, epigyny, crowding of small flowers into bracteate spikes or heads, porous anther dehiscence, and parietal placentation in monolocular ovaries.

Buxineae

Most primitive in their wood anatomy are the members of the Buxineae (or Buxales), including the archaic, widely distributed Buxaceae (the only family with some New World representation) (Carlquist, 1982) and monogeneric Didymeleaceae of Madagascar, Daphniphyllaceae of eastern Asia and Malesia, and Balanopaceae of Australasia. The primitive xylem of members of this suborder is distinguished by the very small, long to medium vessel elements, exclusively solitary and with 15- to 30-barred scalariform perforation plates, and very small, scalariform to opposite or transitional intervascular pitting; xylem parenchyma diffuse and apotracheal; rays markedly heterocellular, 2 to 4 cells wide with numerous uniseriates; and tracheids or fiber-tracheids, very short to moderately long, with large to small bordered pits. Except for some suffrutescent perennials or shrubs in the Buxaceae and some shrubs in the Daphniphyllaceae, most members of the Buxineae are small trees of tropical to warm temperate, mesic forests with evergreen, exstipulate, simple, pinnately-veined, mostly glabrous and entire leaves. The flowers are much more specialized than the xylem and rather reduced, being unisexual though often possessing nonfunctional staminodia or pistillodia. The species are either monoecious or dioecious. The flowers are apetalous or naked, in tight bracteate racemes or spikes. The sepals, when present, are imbricate and usually four in number. Stamens are usually four to six, rarely numerous or reduced to two, with large anthers dehiscing by longitudinal slits. The gynoecium is syncarpous, abortive in or absent from male flowers, with three or two carpels and locules (apparently reduced to one in *Didymeles* Thou.), each usually with two anatropous ovules, bitegmic and crassinucellar, pendulous from the apex of each locule. The fruit is a loculicidally dehiscent capsule or drupe, and the seeds usually have a straight, axile embryo in copious fleshy endosperm (much reduced in *Balanops* Baill. or entirely absent in *Didymeles*).

Didymeles, as also some Buxaceae, is reported to have encyclocytic stomata (stomata surrounded by a rosette of subsidiary cells) (Koehler, 1980). Koehler also stressed the palynological similarities of *Didymeles* with members of the Buxaceae. The stomata of *Daphniphyllum* Blume and *Balanops* are paracytic or laterocytic. The alternate, evergreen, leathery leaves of these two latter genera are commonly subverticillate at the ends of the branches much as in some species of Pittosporaceae. Unlike members of the Buxaceae but similar to some pittosporums, species of *Balanops* and *Daphniphyllum* have an ovary that is imperfectly septate into 4–2 locules (with placentation thus parietal). The four families of the Buxineae are readily separable with their own suites of distinctive features and specializations due to evolutionary divergence, but they do appear to form a monophyletic group with probable common Cretaceous ancestry.

Pittosporineae

The essentially Australasian Pittosporineae with the three families Pittosporaceae, Tremandraceae, and Byblidaceae retain the least specialized flowers but have the most specialized xylem in the order. The Pittosporaceae, with nine genera and about 200 species, are mostly restricted to Australasia except for the large genus *Pittosporum* Banks ex Soland. apud Gaertn., whose wide range (Thorne, 1973) from southern Africa and Macaronesia to Japan and Polynesia nearly encompasses the total range of the order with the exception of the New World species of Buxaceae. Members of the family have typically actinomorphic, bisexual, pentamerous flowers with biseriate perianth of usually distinct, imbricate parts, and superior ovary with 2–5 complete or incomplete locules and numerous ovules on axile or parietal placentae.

The xylem of many Pittosporaceae (Carlquist, 1981) has vessel elements with simple perforation plates and alternate, small intervascular pitting; sparse, paratracheal parenchyma; almost homocellular rays with few uniseriates, and moderately-short, septate libriform fibers with simple or vestigially bordered pits. At least one of the New Caledonian species of *Pittosporum, P. paniense* Guill., has more primitive xylem with scalariform pitting on the vessel elements. It is significant that New Caledonian species among others also have subverticillate foliage much like that of species of *Balanops* and *Daphniphyllum* (Carlquist, 1980; Huang,

1965), similar incomplete septation and parietal placentation in the pistils, and an unusual mode of crystal occurrence, with "ray cells subdivided into cells each of which bears a rhomboidal crystal." Similar crystals are also found in *Balanops,* Tremandraceae, Brunineae, and the Hamamelidaceae (Carlquist, 1977b, 1977c, 1980), with which the Pittosporales share both primitive evolutionary level of wood anatomy and common ancestry in the Rosanae (formerly Rosiflorae).

The Australian Tremandraceae and Byblidaceae (Carlquist, 1976b, 1977c) were accepted by Dahlgren (1983) as part of his Pittosporales but Cronquist (1981) and Takhtajan (1987) place the Tremandraceae in their Polygalales, presumably because of stem anatomical features and poricidally dehiscent stamens. Carlquist (1977c), however, found tremandraceous wood anatomy to be remarkably similar to that of the Pittosporaceae. Also poricidal stamens are found in all three families of Pittosporineae (along with many other Australian taxa pollinated by hover flies). These three families must be closely related and stem from common Australian ancestry.

Brunineae

A somewhat more diverse suborder are the Brunineae, a group of primarily South African mesic relicts of mountainous areas including Bruniaceae, *Geissoloma* Lindl. ex Kunth, *Grubbia* Endl., *Myrothamnus* Welw., and *Roridula* Burm. f., plus the aquatic *Hydrostachys* Thou., also of South Africa but ranging north into tropical Africa and Madagascar. Each of these listed genera form monotypic families, distinct enough to be placed in separate, widely unrelated orders by other phylogenists. Carlquist (1975, 1976a, 1976c, 1977a, 1977b, 1978a, 1978b) has, however, studied very thoroughly the wood anatomy and relationships of these taxa and found them to be very similar both in the archaic xylem features and in features unrelated to specialization level such as the subdivided ray cells with rhomboidal crystals (Bruniaceae, *Geissoloma,* and *Grubbia*), plus striking similarities in floral morphology, embryology, and palynology. *Roridula* and *Myrothamnus* species are somewhat less similar in wood anatomy as well as in growth habit although all these South African plants are mesic shrubs.

Most divergent are the species of *Hydrostachys,* peculiar pin-

natisect-leaved, tuberous-stemmed hydrophytes specialized for life in seasonal streams. Yet even these species share with *Myrothamnus* species, some also reaching Madagascar, leaves with dilated bases; imperfect, naked flowers each sessile in the axil of a bract in a tight spike; dioecism; syncarpous pistil with divergent styles; similar pollen grains united in tetrahedral tetrads; and fruit a many-seeded, small capsule. Surely these African–Malagasy taxa share enough characteristics to merit treatment in the same suborder or order. At the very least, they deserve the same careful, objective study of their morphology and relationships as given their stem anatomy by Carlquist, as cited above.

STILBACEAE

Another pair of somewhat more specialized South African taxa that are illustrative of the doctrine of geographic plausibility are the Stilbaceae and the genus *Retzia* Thunb. Both taxa were long buried in other families, the stilboids in the Verbenaceae and *Retzia* in the Loganiaceae. Both groups consist of woody shrublets with narrow, verticillate, sclerophyllous leaves, and both are restricted to the Cape Region of the Republic of South Africa. They have startlingly similar xylem anatomy (Carlquist, 1986), pollen grains, and iridoid glucosides (Dahlgren et al., 1979), two of which, unedoside and stilbericoside, are found in both *Retzia* and *Stilbe* Bergius. These and other morphological similarities command treatment of these two groups in the same family, the conserved Stilbaceae, probably as distinct subfamilies, possibly most closely related to the Buddlejaceae of the Bignoniales.

ARCHAIC ANGIOSPERMS

Southeastern Asia and adjacent Malesia and Australasia have an inordinately large number of relict angiosperms, especially in the two superorders Annonanae and Rosanae (including Hamamelidanae). This richness in relicts abounding in primitive characteristics had led to an argument among botanists as to whether the area is the center of origin of the Angiospermae or is merely a great natural museum, or refugium, where unspecialized angiosperms and other vascular plants have been able to survive great climatic changes and other catastrophic events. Our inadequate knowledge of the fossil record and of tectonic events when the

angiosperms evolved makes it impossible to determine at present the place of origin of the angiosperms. Also we know that the area in question was divided in Cretaceous time into two major and several minor tectonic plates and that the Australasian and southeastern Asiatic plates were widely distant from each other.

It is possible that some of the relicts in eastern Malesia and Australasia may have immigrated to those areas from southeastern Asia after the two great plates came together in the Miocene some 15 million years ago (Thorne, 1978a). Certainly southeastern Asia, Malesia, and Australasia have long been great natural refuges for archaic plants in their dissected, moist, habitat-rich mountainous areas and isolated archipelagos. Also like the Guayana and Brazilian highlands, Africa, Madagascar, and other areas, eastern Asia and Australia have independently been major centers of origin and evolution for the angiosperms.

ANNONANAE (formerly ANNONIFLORAE)

Perhaps most characteristic of the Asiatic–Malesian–Australasian regions are the numerous members of the Annonanae (Thorne, 1974) in which I now include the orders Annonales, Nelumbonales, Paeoniales, and Berberidales. This rather large group of relatively unspecialized flowering plants contains, in my opinion, the most archaic and least specialized of all angiosperms.

Winteraceae

Probably retaining the largest suite of primitive characteristics are the ancient Winteraceae (Thorne, 1972, 1978b) with their highly disjunct Gondwanaland distribution pattern and a fossil record reaching back into early Cretaceous time (Walker et al., 1983). Among their more primitive (plesiomorphic) features are their woody habit with leaves simple, alternate, pinnate-veined, entire, petiolate, glabrous, evergreen, and exstipulate, with paracytic stomata and rather primitive leaf architecture; entirely vesselless wood, long fusiform cambial initials and tracheids, heterogeneous rays, and diffuse xylem parenchyma; bisexual, actinomorphic flowers with poorly differentiated perianth parts and variable number of mostly separate, spirally arranged organs; undifferentiated broad microsporophylls with lateral to apical, protuberant microsporangia; pollen grains distally mono-aper-

turate; carpels styleless megasporophylls with partly free margins forming conspicuous double stigmatic crests; anatropous, crassinucellate, bitegmic ovules on marginal or submarginal placentae; and embryo rudimentary in abundant endosperm.

The Winteraceae have their great center of preservation, and perhaps development, in Australasia especially in the highlands of New Caledonia, that island treasurehouse of archaic relicts. Four of the eight currently accepted genera are well represented there, two of them endemic. A fifth genus is endemic to New Zealand and another to South and Central America from Fuegia and the Juan Fernandez Islands north to Mexico. A seventh was collected once in the rainforests of northern Madagascar, and an eighth is wide-ranging from Tasmania north to Borneo and the Philippines.

Illiciineae

The probable closest relatives to the Winterineae are the Illiciineae, with the two families Illiciaceae and Schisandraceae heavily developed in eastern Asia with a very few species of *Illicium* L. and *Schisandra* Michx. found also in southeastern North America, the former also reaching the Greater Antilles and eastern Mexico. More distantly related to the Winteraceae, but like them primitively vesselless, is the monospecific family Amborellaceae, restricted to New Caledonia.

Austrobaileyineae and Annonineae

Australasia, here broadly defined to include New Guinea, New Caledonia, Fiji, and New Zealand, also harbors another group of Annonalian relicts containing the monotypic Austrobaileyaceae of northern Queensland, intermediate between the Annonineae and Laurineae; the closely related monotypic Himantandraceae and ditypic Eupomatiaceae of eastern Australia and New Guinea, ditypic Degeneriaceae of Fiji, and relatively large, mostly Asiatic family Magnoliaceae, which overlaps the first two in the New Guinea highlands. As is true for the calycanthaceous *Idiospermum* S. T. Blake of northern Queensland, the Winteraceae, and three archaic genera of Hamamelidaceae, the closest relatives of these Australasian plants are in eastern Asia. All of the 12 generally accepted and mostly endemic genera of Magnoliaceae, most of

the Illicineae, the other two genera of Calycanthaceae, and most of the approximately 30 hamamelidaceous genera are represented in eastern Asia. If these relicts had not reached Australasia after the coming together of the Australasian and Asiatic tectonic plates some 15 million years ago, it is hard to understand how such relatively close relatives could have evolved independently on two such widely disjunct continents, one Gondwanic and the other Laurasian.

PAEONIALES

Also centered in eastern Asia are the Paeoniales (Thorne, 1981) including two monogeneric families, Glaucidiaceae with only *Glaucidium palmatum* Sieb. & Zucc. of Japan and Paeoniaceae with 33 *Paeonia* L. species ranging from western Europe and northern Africa to eastern Asia and western North America. The two genera are linked not only by geographic distribution and usual mesic forest habitat but also by their rhizomatous perennial habit, unspecialized xylem, centrifugal initiation and maturation of stamens, apocarpy, low chromosome number ($n = 5$ or 10), and follicular fruit. Their closest relatives seem to be the somewhat more specialized Berberidales, also heavily represented in eastern Asia.

BERBERIDALES

Asiatic relicts of the Berberidales include such monotypic or oligotypic families or subfamilies as the Sargentodoxaceae, Lardizabalaceae, Nandinaceae, Circeasteraceae, Lardizabalaceae, berberidaceous Ranzanoideae, and papaveraceous Pteridophylloideae. All of these taxa are restricted to eastern Asia except the Lardizabalaceae, which quite anomalously have two additional monospecific genera in central Chile (Thorne, 1972). Eastern Asia is well supplied too with most of the subfamilies and many of the genera of three larger families, Menispermaceae, Ranunculaceae, and Berberidaceae. One is tempted to consider eastern Asia the center of origin of this order. Two subfamilies of Papaveraceae, Eschscholzioideae and Platystemonoideae, however, are mostly or exclusively centered in western North America, and the monospecific Hydrastidaceae (Tobe and Keating, 1985), somewhat intermediate between the ranunculads and berberi-

dads, is indigenous only in eastern North America, being the sole endemic family in our Northeast. At the very least, this order can be considered as Laurasian in origin.

NELUMBONALES—NYMPHAEANAE—RAFFLESIANAE

The related but widely distributed aquatic order Nelumbonales (Thorne, 1981, 1983) with the two monogeneric families Nelumbonaceae and Ceratophyllaceae are also indigenous in eastern Asia through Australasia. Likewise represented but more distantly related are the similarly aquatic and widely distributed nymphaeanean Cabombaceae and Nymphaeaceae, the latter with all three subfamilies present and one, the Hydrostemmatoideae (Barclayoideae), restricted to southeastern Asia. Another archaic group probably related to the Annonanae are the Rafflesianae, greatly reduced and specialized internal stem parasites, with three subfamilies present, Rafflesioideae of Indomalesia, Mitrastemonoideae of eastern Asia–Malesia and Central America, and the widely disjunct Apodanthoideae with a species of *Pilostyles* Guill. in Western Australia and another in the asiatic Near East. Unrepresented are the African–Mexican Cytinoideae and the African–South and Central American Hydnoraceae.

HAMAMELIDALES

Among the numerous other relicts of eastern Asia are the Hamamelidales (Thorne, 1976) of the Rosanae (now including my former Hamamelidiflorae). Most archaic in the order are the Trochodendrineae with the primitively vesselless *Trochodendron aralioides* Seib. & Zucc. and *Tetracentron sinense* Oliv. of the Trochodendraceae and the genera *Cercidiphyllum* Sieb. & Zucc., *Euptelea* Sieb. & Zucc., and *Eucommia* Oliv., each representing a monogeneric family. All of these genera, once wide-ranging in the northern hemisphere, are now restricted to eastern Asia. Their common origin is indicated by their similar primitive xylem, leaf architecture, stomatal apparatus, pollen grains, and floral morphology. The fossil evidence for their once wide ranges furnishes a good warning to biologists that we must be aware that present distributions are not necessarily indicative of past distributions. Because some 23 genera (out of perhaps 31 genera) of the closely related Hamamelidineae are restricted to or represented in eastern

Asia, there is a strong possibility that the whole order also had its center of origin in eastern Asia and radiated out from there to other parts of the Laurasian supercontinent in Cretaceous or Paleogene time.

SIMMONDSIACEAE

Closer to home in North America are several indigenous, and mostly endemic, taxa that until recently were misplaced or, in my earlier classifications, were *taxa incertae sedis*. In each case the dictum of geographic plausibility did supply or could have supplied the clue to their proper phylogenetic treatment. *Simmondsia chinensis* (Link) C. K. Schneid. (Thorne, 1985), an abundant evergreen dioecious shrub of the arid Southwest and a newly developed oilseed crop plant (jojoba or goatnut) producing a valuable, liquid wax, was long misplaced in the quite unrelated family Buxaceae. Morphologically *Simmondsia* seems most closely related to the Euphorbiaceae. Kakkar (1973) noted the similarity in leaf architecture of jojoba with that of species of *Euphorbia* L. with special reference to the bundle sheath and thick-walled cells at the vein endings.

However, the principal clue to the relationship was supplied by Scogin (1980), who found serological cross-reactivity between rabbit antiserum to *Simmondsia* seed protein and seed extracts from three species of the euphorbiaceous genera *Sapium* P. Br. of the Euphorbioideae and *Mallotus* Lour. and *Ricinus* L. of the Acalyphoideae. The seed extracts of other tested taxa showed no such cross-reaction. *Simmondsia* and *Sapium biloculare* (S. Wats.) Pax, whose seeds are among the famous Mexican jumping beans, often grow together in the Sonoran Desert. Because of its unique syndrome of chemical and morphological characteristics *Simmondsia* merits treatment as an independent family Simmondsiaceae in the Euphorbiales.

CROSSOSOMATACEAE

Similarly misplaced for more than a century was the genus *Glossopetalon* A. Gray, attributed by its author with some misgivings to the Celastraceae. Re-examination of the genus morphologically and biochemically (Thorne and Scogin, 1978) showed that the genus, with several species indigenous in western North

America, should join *Crossosoma* Nutt. and the recently named genus *Apacheria* Mason in the Crossosomataceae, now a considerably expanded North American family.

The Crossosomataceae have at times been misplaced in the Dilleniinae due to the mistaken belief that the stamen initiation and maturation were centrifugal. It is found thriving commonly side by side with its similarly apocarpous or nearly apocarpous relatives of the Rosaceae, Crassulaceae, Saxifragaceae, and Hydrangeaceae. The insular species *Crossosoma californicum* Nutt., the theme plant of Southern California Botanists, is called Wild-apple by the residents of Santa Catalina Island, where it is often associated with its distant cousin, the rosaceous ironwood tree *Lyonothamnus floribundus* A. Gray.

BATACEAE—GYROSTEMONACEAE—SAPINDACEAE

The Saltwort, *Batis maritima* L., a succulent-leaved sprawling dioecious shrub of our southern sea shores, was long misclassified near the equally halophytic chenopods and amaranths of the centrospermous Chenopodiales. Study of its disjunct monoecious cousin, *Batis argillicola* van Royen of northern Australia and Papua, gave us the clue to its probable relationship to the Australian Gyrostemonaceae and sapindaceous Dodonaeoideae, Stylobasioideae, and Emblingioideae (Thorne 1977; Carlquist, 1978c).

Batis resembles the Gyrostemonaceae, also fugitives from the Centrospermae, in their presumed anemophily; shrubby habit with relatively specialized stem anatomy; linear leaves with minute stipules; presence of glucosinolates or associated catalyzing enzyme; unisexual, apetalous flowers; isopolar, tricolporoidate, pertectate, non-baculate pollen grains; pistil with a single ovule in each locule; and septicidally-dehiscent fruits (in *Batis argillicola*).

The Gyrostemonaceae in turn have in common with the Dodonaeeae, in addition to their overlapping Australian ranges, shrubby habit; alternate, simple, entire, spatulate to commonly linear leaves with anomocytic stomata; apetalous, unisexual flowers with connate calyx 8-4-2-lobed or entire; stamens six to numerous on the top or rim of a convex or discoid receptacle; similar pollen grains; gynoecium of one or two to numerous, connate carpels with mostly free styles; ovary locules each with one axile, campylotropous, bitegmic ovule; fruit an indehiscent nutlet or

schizocarp in which each membranous carpel disperses separately from the others and the discoid axis; and curved seed with small, basal arillode. It is noteworthy that *Batis maritima* on our tropical American shores is closely associated with *Dodonaea viscosa* L. (Sapindaceae), *Scaevola plumieri* (L.) Vahl (Goodeniaceae), *Cassytha filiformis* L. (Lauraceae), and the abundantly naturalized *Casuarina equisetifolia* Forst. (Casuarinaceae), all with ultimately Australasian antecedents.

ADDITIONAL NORTH AND SOUTH AMERICAN EXAMPLES

Many additional examples to show the efficacy of the principle of geographic plausibility could be discussed were space available. In North America one could list in addition the contiguity in the Southwest of the Fouquieriaceae (sometimes classified near the Old World Tamaricaceae) with the related Ericaceae and Ebenaceae; the anemophilous Garryaceae with the Cornaceae, Nyssaceae, and Alangiaceae (the last two families now extinct in the Southwest); and the Krameriaceae with the probably related Polygalaceae and the more completely tropical Trigoniaceae and Vochysiaceae.

Moving south to South America we could list for the Guayana Highlands the closely associated and related sarraceniaceous *Heliamphora* Benth. and Marcgraviaceae, Bonnetiaceae, Clusiaceae, and other thealean taxa; and commelinalean *Thurnia* Hook. f., Rapateaceae, Xyridaceae, and terrestrial Bromeliaceae. Farther south in Brazil there is heavy development of the closely related Mayacaceae and Commelinaceae and of the distantly related Velloziaceae and Pontederiaceae. The tropical American–African Canellaceae is commonly associated with many species of the related Annonaceae and Myristicaceae. In temperate South America one could cite as related and associated the Gomortegaceae, Lauraceae, and Monimiaceae; Malesherbiaceae, Caricaceae, Turneraceae, and Passifloraceae; Tropaeolaceae and geraniaceous Vivianioideae and Ledocarpoideae; and lilialean Philesiaceae and Alstromeriaceae.

Similar suites of related taxa could be listed for the other continents and the great island refugia of Madagascar and New Caledonia in addition to those taxa already discussed above. In developing my own classification plant geographic data have thus been most valuable in seeking out phylogenetic relationships, when used in conjunction with paleobotanical, host-parasitic, se-

rological, and comparative biochemical information as well as the usual morphological information gleaned from comparative studies of flowers, pollen grains, fruits, seeds, xylem and other stem anatomy, and leaf architecture. Two new approaches that show great promise in the study of angiosperm phylogeny are molecular taxonomic studies of chloroplast DNA and nuclear ribosomal DNA and cladistic methodology.

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